

## 6.

Sexual Dimorphism in the Skeletal Elements of the Gonopodial Suspensoria in Xiphophorin Fishes.<sup>1</sup>

MYRON GORDON &amp; PAUL BENZER.

*New York Aquarium.*

(Plate I; Text-figures 1-11).

This survey of the sex-modified hemal and interhemal spines that make up the gonopodial suspensorium in xiphophorin fishes was made to serve several purposes. These skeletal elements were found anew by Howell Rivero and Hubbs (1936) to be of importance in the classification of viviparous cyprinodonts in general; therefore, it is hoped that definitive descriptions of these bones in each of the seven xiphophorin species might reveal relationships in this small but difficult taxonomic group not previously appreciated. Recent work by Turner (1942) and by Cohen (1942), reported by Gordon, Cohen and Nigrelli (1943), has also shown that these structures in immature fishes are extremely sensitive to synthetic sex hormones; thus it is necessary for future endocrine studies to define the normal and final stages in untreated males of each species for comparative purposes. Finally, the standard types of the gonopodial suspensorium elements are required for possible genetic analysis of species and generic differences, for in this group hybridization, under laboratory conditions, is the rule rather than the exception. Heretofore no comprehensive study of these elements has been made of the seven xiphophorins now known, although Langer (1913) has shown these structures beautifully in two of them: *Xiphophorus hellerii* and *Platypoecilus maculatus*.

## MATERIAL AND METHODS.

Fully developed males of three species of *Xiphophorus* and four species of *Platypoecilus* were studied. The original stocks of the seven xiphophorin species were collected in 1939 and 1940 by two New York Aquarium expeditions. The stocks have been

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maintained at the New York Zoological Society's laboratories. Many of the stocks are in their seventh generation.

The specific sites from which the living material has been collected are given on page 58, together with the number of each species used and the standard size limits in millimeters.

Further details of the distribution of these species and the ecological conditions of their various habitats are given by Gordon (1940, 1943).

Whole fish were fixed in 95% alcohol, cleared in 2% potassium hydroxide to which a 3% solution of hydrogen peroxide was added. They were stained in Alizarine Red S and mounted and studied in glycerine. The technique followed was Benzer's (1940) modification of the method of Schultz (1897). This treatment made the muscles transparent, with all the tissues intact, while the bones are specifically stained.

The areas of the gonopodial suspensorium were photographed. Enlargements were made on 8" x 10" semi-matte paper. The critical elements were outlined with waterproof ink, then the prints were bleached in potassium ferro-cyanide solution. Final tracings were made from these drawings.

## GENERAL DESCRIPTION OF THE GONOPODIAL SUSPENSORIUM IN THE XIPHOPHORINI

The gonopodial suspensorium consists of the masculinized hemal spines (gonapophyses) and the masculinized interhemal spines (gonactinosts) that are associated with the anal fin (gonopodium). Between the points of articulation of the gonactinosts and the bases of the rays of the gonopodium, there are two series of tiny pterygial elements. These provide the pivotal elements upon which the gonopodium is enabled to swing in all directions.

*The Gonapophyses (the masculinized hemal spines).*

The most anterior hemal spines, usually

Species	Size		Habitat of Original Stock
	No. in mm.		
<i>Platypoecilus couchianus</i>	18	21-26	Spring pool at St. Catarina, Nuevo Leon
<i>Platypoecilus xiphidium</i>	25	20-33	Spring pool at Cruz, Tamaulipas
<i>Platypoecilus variatus</i>	21	18-34	El Nilo, Rio Tambaon, San Luis Potosi
<i>Platypoecilus maculatus</i>	13	20-25	Plaza de Agua, Rio Jamapa, Veracruz
<i>Xiphophorus pygmaeus</i>	16	18-23	Rio Axtla at Axtla, San Luis Potosi
<i>Xiphophorus montezumae</i>	14	26-43	Arroyo Palitla, Tamazunchale, San Luis Potosi
<i>Xiphophorus hellerii</i>	12	32-45	Arroyo Zacatispan, San Bartolo, Oaxaca.

three in number, are modified into gonapophyses. Unlike normal spines they are directed forward rather than backward. Some gonapophyses are as straight as unmodified hemal spines while others are slightly bowed, deeply arched or sigmoid. Some gonapophyses are no broader than hemal spines while others are at least twice as broad, indicative of greater strength and larger surface for the insertion of gonopodial muscles. The first gonapophysis is the shortest. The most posterior gonapophysis (usually the third) is the longest, being as long as, or longer than, its adjacent unmodified hemal spine. The second gonapophysis is intermediate in length. All gonapophyses have concave posterior contours.

The first gonapophysis arises from the thirteenth vertebra and its tip is directed just anterior to the end of the seventh actinost. The tip of the second gonapophysis lies just posterior to the eighth actinost. The distal tips of the ninth and tenth actinosts are encompassed by the terminal points of the second and third gonapophyses.

The first gonapophysis usually bears the last rib, but ribs may be borne, particularly in some species of *Xiphophorus*, on the second and on the third gonapophysis.

*The Ligastyle (bone in the suspensory ligament).*

A spinous ligament connects the ventral surface of the centrum of the tenth vertebra with the distal portion of the fused gonactinosts 2, 3 and 4. The spine which lies embedded within the ligament has been shown by various workers to be the modified first hemal spine originating on the twelfth vertebra. In ontogeny it breaks away from its hemal arch, becoming much thinner; it is forced anteriorly a distance of two vertebrae. Being a thin, spinous bone within a ligament, the term "ligastyle" is suggested for it.

*The Gonactinosts (the masculinized actinosts).*

The actinosts or interhemal spines are nine in number. They are variously modified in the gonopodial suspensorium complex. The first, and most anterior gonactinost is

free, small and rod-like; it is directed more anteriorly than dorsally.

The second, third and fourth gonactinosts are variously fused to form the gonactinost complex proper. The second and third gonactinosts may be fused suturely at their bases. The third and fourth are always fused at their bases. The posterior surface of the fourth gonactinost is concave. This concavity serves as a grooved area in which the fifth gonactinost is moved in a directed path. The fifth element is not fused to any other; it is shaped like a bow and its middle convex portion slips within the concave trough of the preceding gonactinost complex. Only the ends of the fifth element are visible from the lateral aspect.

The sixth, seventh, eighth and ninth actinosts form a series of simple, slightly curved rods which are evenly spaced; they become smaller and weaker progressively towards the posterior. They do not appear to be greatly modified.

The fusion of some gonactinosts, the increased strength of some and the weakening of others, is reflected, in some measure, to the conditions found in the rays of the gonopodium. In the latter, rays 3, 4 and 5 are tremendously strengthened while the others are generally smaller and weaker than their unmodified counterparts as seen in the anal fins of females.

#### GENERIC DISTINCTIONS.

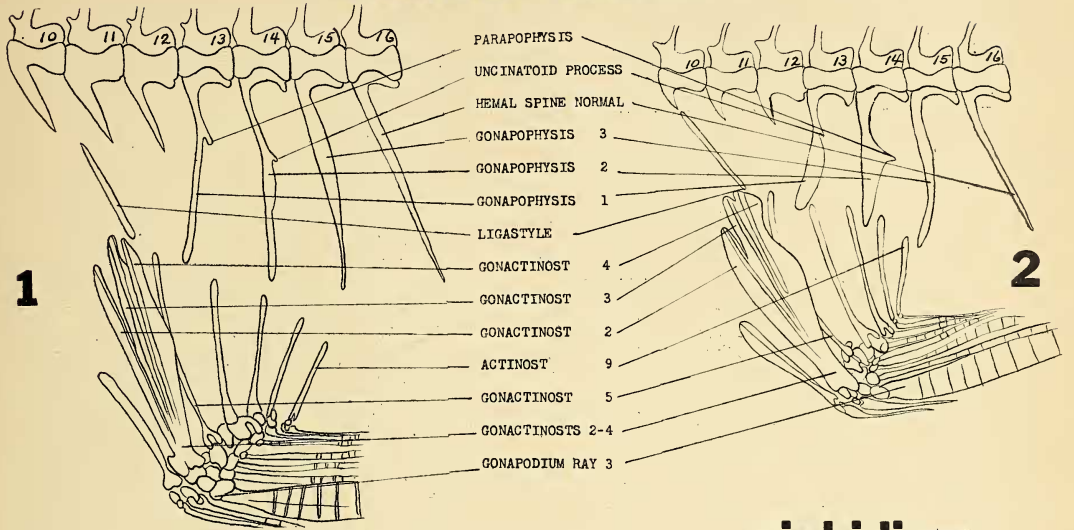
Several general differences in the configuration of the element of the gonopodial suspensoria exist between the members of the genus *Xiphophorus* and those of *Platypoecilus*, see Table II.

*Extent of Fusion of the Gonactinosts.*

Fusion of the gonactinosts may take place at their bases, at their tips, at their bases and tips leaving the mid-section separate, or the elements may fuse for their entire length.

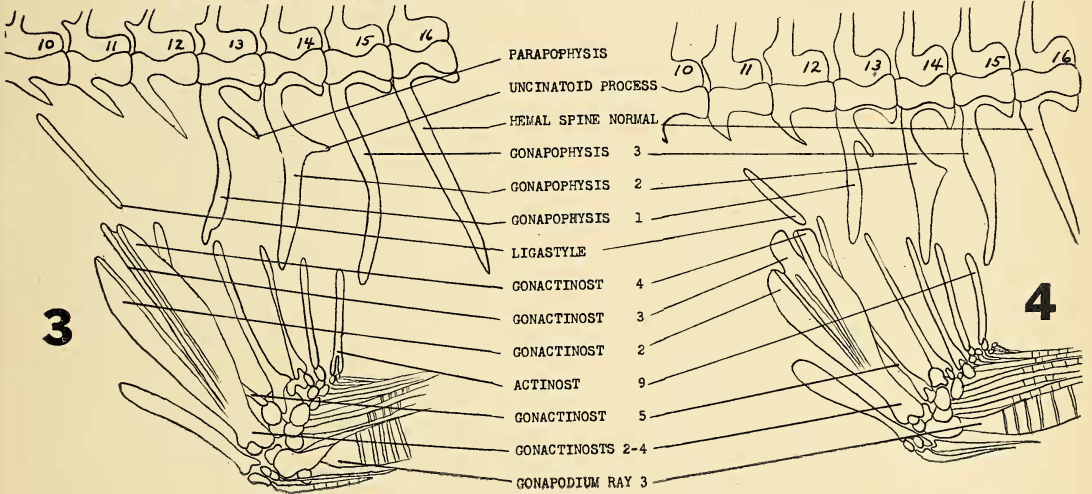
While there is general fusion of some of the gonactinosts 2, 3 and 4 in all xiphophorins, fusion is much more extensive in the swordtails than in the platyfishes. For example, the tips and bases of rays 3 and 4 are rarely fused in *Platypoecilus* species; they are rarely separate in *Xiphophorus*.

# PLATYPOECILUS



**maculatus**

**xiphidium**



**variatus**

**couchianus**

TEXT-FIGS. 1-4. Comparative morphology of the gonopodial suspensoria of the four species of *Platypoecilus*.

### The Rib-Gonapophysis Relationships.

In all species of *Platypoecilus*, the first gonapophysis bears the last pair of ribs. In the swordtails no such uniformity exists. In *Xiphophorus pygmaeus* the rib gonapophysis relationship is the same as in the platyfishes; that is, the first gonapophysis carries the last pair of ribs. In *X. montezumae* the second gonapophysis bears the last pairs of ribs, while in *X. hellerii* the third gonapophysis presents the last pair of ribs.

### SPECIFIC DISTINCTIONS IN *Platypoecilus*.

#### The Second Gonapophyses.

The differences in the elements of the gonopodial suspensoria of the platyfishes may be expressed quantitatively, see Tables I, II. The gonapophyses are small, the largest measuring only 3 mm., and their extensions, the parapophyses of the first and the uncinatoid processes of the second gonapophyses, are smaller still. Nevertheless an

TABLE I. Analysis of the Second Gonapophyses in *Platyopocilus* Males.

Each number represents in millimeters the measurements of the gonapophyses and their processes of three specimens, averaged.

The second set of values: a, b, c, d, represents the average measurements of A, B, C, D, in proportional parts of A.

<i>Species of Platyopocilus</i>	<i>Length of gonapophyses</i>	<i>Length of uncini</i>	<i>Spread of uncini tips</i>	<i>Width of gonapophyses</i>	
	A	B	C	D	
<i>maculatus</i>	2.53	0.97	1.00	0.53	
<i>variatus</i>	1.93	0.97	1.33	0.40	
<i>xiphidium</i>	2.56	1.13	0.73	0.72	
<i>couchianus</i>	2.07	0.97	1.13	0.40	
	A	B	C	D	c
	a	A	A	A	d
<i>maculatus</i>	1.00	0.38	0.39	0.21	1.9
<i>variatus</i>	1.00	0.50	0.53	0.21	2.5
<i>xiphidium</i>	1.00	0.45	0.28	0.28	1.0
<i>couchianus</i>	1.00	0.47	0.55	0.19	2.9

attempt was made to record their proportions accurately.

The uncinus of the second gonapophyses is least developed in *P. maculatus* (0.38) and is increasingly stronger in *P. xiphidium* (0.45), *P. couchianus* (0.47) and *P. variatus* (0.50). For these values the lengths of the second gonapophysis served as a standard. It was measured from the mid-point of the centrum to its ventral tip. The extent of the posterior projection of the uncinus was obtained by measuring the distance between the anterior margin or keel of the second gonapophysis and the most posterior limit of the uncinus.

While on the whole the lengths of the uncini are much alike in the four species, they differ in the manner in which they spread away from the keel of the gonapophyses. For example, in *P. xiphidium* the uncini point directly toward the posterior while in the others they flare out at various angles. This degree of spread of the terminal points of the uncini has been measured by comparing the spread with the length of the gonapophysis; it was least in *P. xiphidium* (0.28), increasing in *P. maculatus* (0.39), *P. variatus* (0.53), *P. couchianus* (0.55).

Anterior views of disarticulated vertebrae with their second gonapophyses indicate that there are considerable species differences in the widths (possibly also denoting degrees of strength) of the modified hemal spines. When the measure of their widths is divided into the measure of their lengths, the following values were obtained: *P. couchianus* has the least width (0.19); it is greater in *P. maculatus* (0.21) and *P. variatus* (0.21), greatest in *P. xiphidium* (0.28). It will be noticed that this relationship is just the opposite of the width of

spine relationship. It may be that the area available for muscle attachments is about the same in all species but in *P. xiphidium* the attachment areas are mainly represented by the wide hemal spines whereas in *P. couchianus* these areas are furnished by the widely flaring uncini.

#### *The First Gonapophyses.*

If the length and the width of the first gonapophyses be compared, it becomes evident that *P. xiphidium* has the widest spine and *P. variatus* the narrowest. If these two measurements are related to the degree of spread of the parapophyses' terminal points, another feature of difference becomes evident: *P. variatus* has the greatest spread while *P. xiphidium* has the least.

#### SPECIFIC DISTINCTIONS IN *Xiphophorus.*

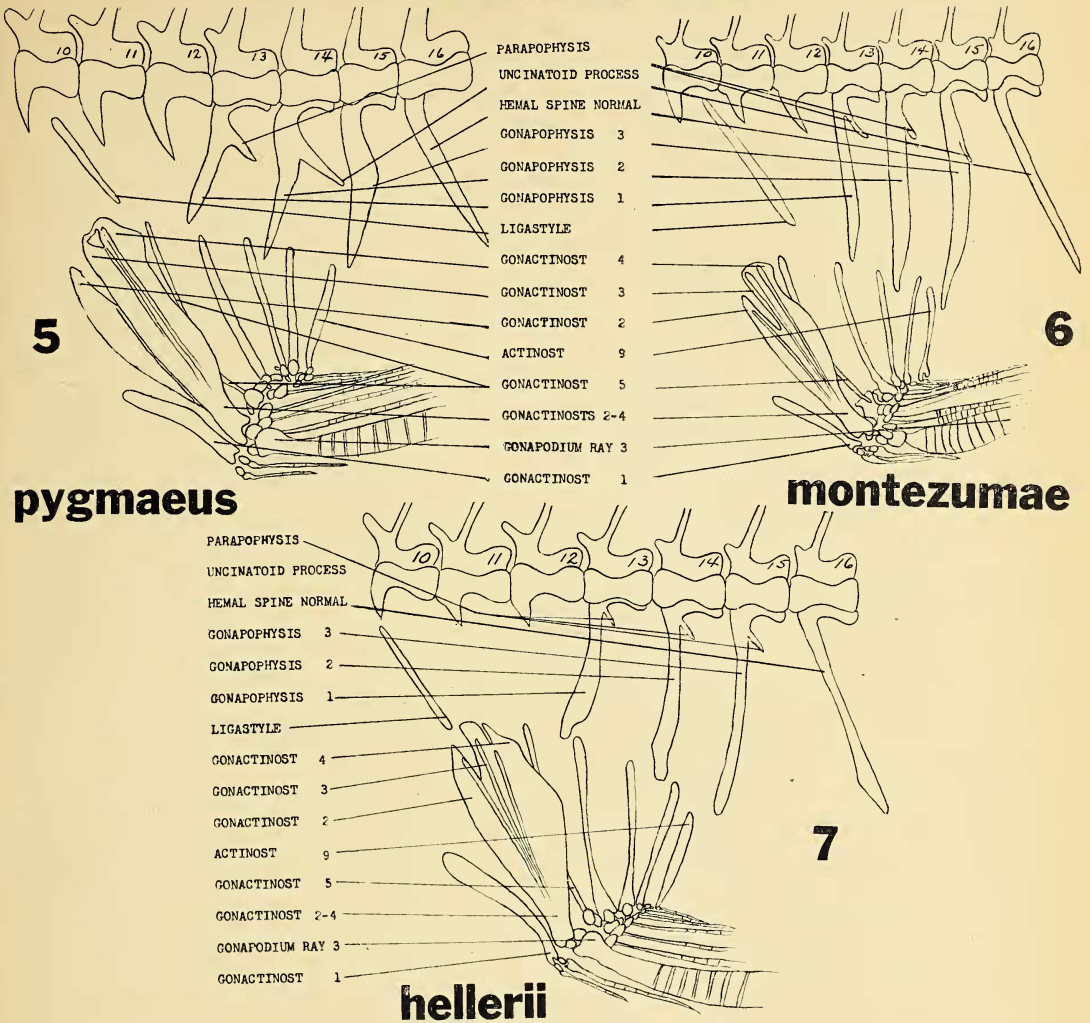
As stated under "The Rib-gonapophysis Relationships," *X. pygmaeus*' first gonapophysis bears a rib. *X. montezumae*'s first and second gonapophyses bear ribs. And *X. hellerii* has ribs coming off the first, second and third gonapophyses. See Table II.

The parapophyses of the first gonapophysis are long in *X. pygmaeus*; they are extremely short in *X. montezumae* and *X. hellerii*.

The uncini of the second gonapophysis are long in *X. pygmaeus* and their counterparts, the parapophyses of the second modified hemal spines are quite short in *X. montezumae* and *X. hellerii*.

The third gonapophysis of *X. pygmaeus* bears neither parapophyses nor uncini; that of *X. montezumae* bears tiny uncini, while that of *X. hellerii* bears small parapophyses which support a pair of ribs.

# XIPHOPHORUS



TEXT-FIGS. 5-7. Comparative morphology of the gonopodial suspensoria of the three species of *Xiphophorus*.

## ANOMALIES IN THE ELEMENTS OF THE GONOPODIAL SUSPENSORIA.

### *P. maculatus*.

In three out of eleven specimens studied in great detail, the second gonapophyses bore only single uncini instead of normal pairs. In these instances the unpaired uncinus arose from nearer the mid-region of the gonapophysis than the lateral section.

### *P. xiphidium*.

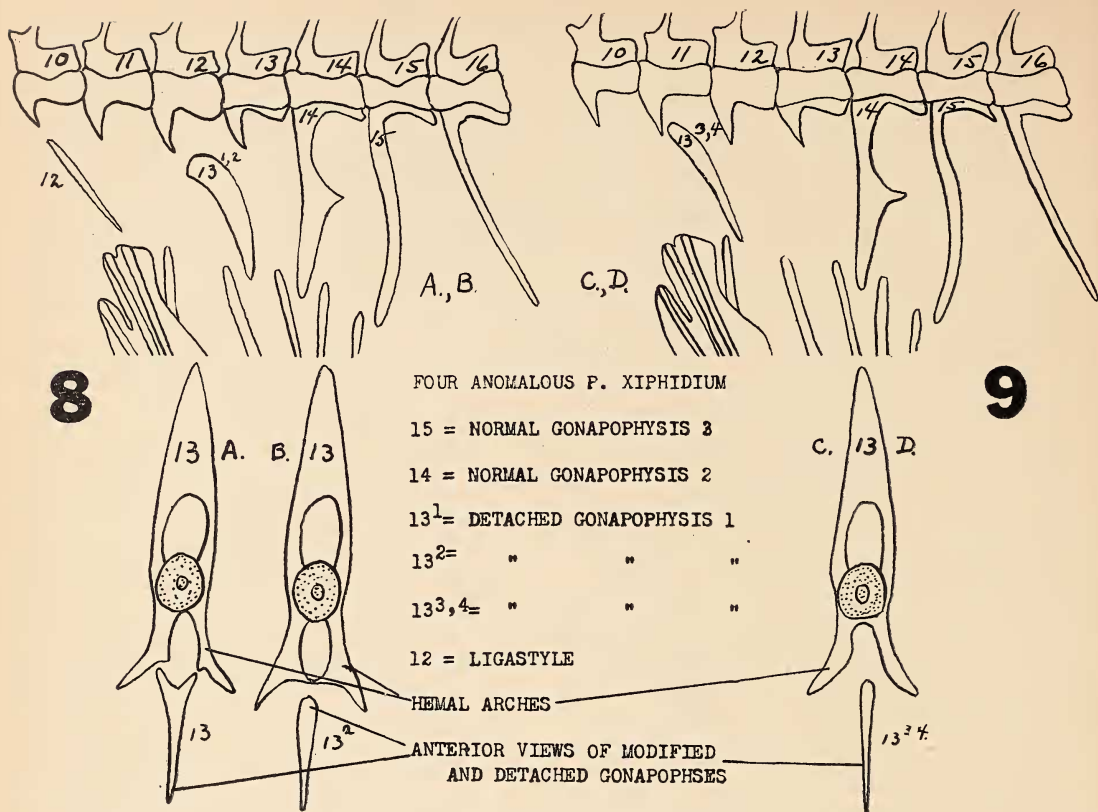
In two out of eighteen specimens the ligastyles were missing. In the same specimens the first gonapophyses were detached from their hemal arches at the thirteenth vertebrae; they were found further forward below the eleventh abdominal vertebrae. This

may represent an instance of substitution, the gonapophyses taking the place of the wanting ligastyles.

In two other specimens the first gonapophyses were also detached and located a distance of two vertebrae forward of their normal position. The ligastyles of these fish were atrophied and they too were forward of their normal position, being found below the ninth instead of the tenth vertebrae.

### *P. couchianus*.

In eight out of eleven specimens the uncini of the second gonapophyses were unequally developed. In these non-symmetrical gonapophyses one of the pair of uncini was normal while the other was variously shortened and scalloped along the posterior edges.



TEXT-FIGS. 8-9. *Platypoecilus xiphidium*. The anomalous elements in the gonopodial suspensorium.

In three specimens the right uncini were the shorter; in five the left ones were smaller. Owing to the fact that eight out of eleven specimens were unsymmetrical with reference to the second gonapophysis it may be more properly said that the symmetrical condition is the anomalous one.

#### *X. hellerii*.

In six out of ten specimens the anterior facet of the tip of the fourth hemal spine is slightly flattened and broadened; this may be indicative of a partial transformation of a normal hemal spine to a gonapophysis.

#### DISCUSSION.

##### *Historical Review of the Gonopodium and its Suspensorium.*

The various elements of the gonopodial suspensorium were first described briefly in *Gambusia* by Ryder (1885) during a period of popular interest in the subject of viviparity in our native fishes. Garman in his extensive study, "The Cyprinodonts" (1895), figured the gonapophyses of seventeen species, remarking: "A peculiar modification of several of the vertebrae is to be

noticed on males of some species in which the anal fin is modified and carried forward; an inferior process from the centra of two or more of the vertebrae over the hinder portion of the body cavity is sent down to furnish support for the base of the transformed fin." In *Xiphophorus*, Garman said that there were four or five modified inferior processes which he called "stays." Later Phillippi (1909) called these "stays" *gonapophyses*, a term which has since been used in referring to the modified hemal spines in cyprinodonts.

Garman referred to the "subvertebral processes" characteristics in distinguishing *Xiphophorus* from *Mollienisia* and *Poecilia*. Phillippi studied the relationships of *Glaridichthys* (now = *Phalloptychus*) *januarius* to *Glaridichthys* (now = *Cnesterodon*) *decemmaculatus*. In his studies he referred not only to gonopodial suspensorium characters but to those of the modified anal fin to which he gave the name of *gonopodium*. The taxonomic value of the male's anal fin had been known previously. Heckel (1848) illustrated his newly described *Xiphophorus hellerii* showing its modified anal fin; the generic name, *Xiphophorus*, was coined with refer-

TABLE II. Evaluation of the Xiphophorin Gonopodial Suspensoria.

	1st Gonapophysis	2nd Gonapophysis	3rd Gonapophysis	Gonactinosts 2-3-4
<i>P. maculatus</i>	Hardly modified Width normal Parapoph. small Bears last RIB	Hardly modified Width normal Uncinus tiniest	Hardly modified Straight No uncinus	2-3 never fused at tips 3-4 never fused at tips 4 no "collar"
<i>P. variatus</i>	Greatly modified Thin, bowed Parapoph. longest Bears last RIB	Greatly modified Width nor., bowed Uncinus longest	Slightly modified Bowed No uncinus	2-3 never fused at tips 3-4 never fused at tips 4 no "collar"
<i>P. xiphidium</i>	Modified Width greatest Parapoph. tiniest Bears last RIB	Modified Width greatest Uncinus long	Slightly modified Bowed No uncinus	2-3 never fused at tips 3-4 never fused at tips 4 "collar" small
<i>P. couchianus</i>	Greatly modified Wider Parapoph. long Bears last RIB	Greatly modified Narrowest Uncinus long	Slightly modified Bowed No uncinus	2-3 never fused at tips 3-4 never fused at tips 1 "collar" small
<i>X. pygmaeus</i>	Greatly modified Tip far forward Parapoph. great Bears last RIB	Greatly modified Tip far forward Uncinus greatest	Modified Broadest No uncinus	2-3 never fused at tips 3-4 usually fused at tips 1 "collar" pronounced
<i>X. montezumae</i>	Hardly modified Tip down Parapoph. small Bears a RIB	Hardly modified Tip down Parapoph. small Bears last RIB	Hardly modified Longest, bowed Uncinus tiny	2-3 never fused at tips 3-4 usually fused at tips 4 "collar" small
<i>X. hellerii</i>	Hardly modified Tip forward, broad Parapoph. small Bears a RIB	Hardly modified Tip broadened Parapoph. small Bears a RIB	Hardly modified Tip blunt Parapoph. small Bears last RIB	2-3 never fused at tips 3-4 usually fused at tips 1 "collar" small

ence to this fin. Poey (1854) figured and described the modified anal fin of *Girardinus metallicus*. Further historical details concerning gonopodia are given by Howell Rivero and Rivas (1944). The work of Langer (1913) will be referred to in some detail.

Kuntz (1913) figured and described the gonopodium and its suspensorium in *Gambusia affinis*. His work was extended by Collier (1936) who stressed the mechanism of gonopodial action in courtship behavior.

#### The Ligastyle.

The origin of the ligastyle has been worked out in great detail by Turner (1942). He showed that in the course of development in the female *Gambusia affinis*, the first hemal arch stemming from the thirteenth vertebra dissolves and its hemal spine is forced forward a distance equal to the lengths of two vertebrae.

Garman (1895) first noticed the relationship of an anterior subvertebral element of the suspensorium to the air bladder, saying that the "stays" divide the posterior portion of the air bladder into separate chambers. Phillipi (1909) called attention to Garman's observations and added that he no-

ticed a "skeletalstab" in *G. januarius* male which was detached from the skeleton proper and located in the notch of the air bladder just posterior to the forked section. Langer (1913) definitely related the "skeletalstab" to one of the hemapophyses, or hemal spines, in incompletely developed male *Xiphophorus* and *Platypoecilus*. These were figured. He explained that the tiny bony elements separate from the subvertebral region of the centra by the thinning of the bony structures and become embedded in ligaments. Langer figured the long ligastyle of *Petalsomus* (= *Alfaro*) *cultratum*, indicating that it is hardly modified from the normal hemal spine. He agreed with Phillipi that *Gulapinnus* does not have a typical ligastyle and adds the following species as lacking one: *Anableps anableps*, *Poecilia heteristia* and possibly *Poecilia vivipara*. However, in *Poecilia amazonica* he found instead of the usual ligastyle four irregular ossicles (*Knochenstuechen*) within the ligament.

An interesting parallelism concerning the history of the ligastyle in *Gambusia* was found in some anomalous specimens of *Platypoecilus xiphidium*. In two adult males no ligastyles were found. Their places were taken by detached hemal spines stemming

from the thirteenth vertebrae. They too had been moved forward a distance equal to the lengths of two vertebrae.

In two other *P. xiphidium* adult males, the ligastyles were found but they were atrophied. Here, too, their places were taken by the detached hemal spines of the thirteenth vertebrae. The detached hemal spines were hardly modified in some while in others they approached the slim stilus contours of typical ligastyles. When the detached spines were dissected and placed back to their presumed point of origin beneath the thirteenth vertebrae they fitted fairly well into the remaining parts of the hemal arches, Figs. 8, 9. In the specimens lacking their normal ligastyles, the detached hemal spines did not restore completely the normal arrangement when applied to the vertebrae of their origin, Figs. 8, 9.

#### *Sexual Dimorphism Expressed in Hemal Spines.*

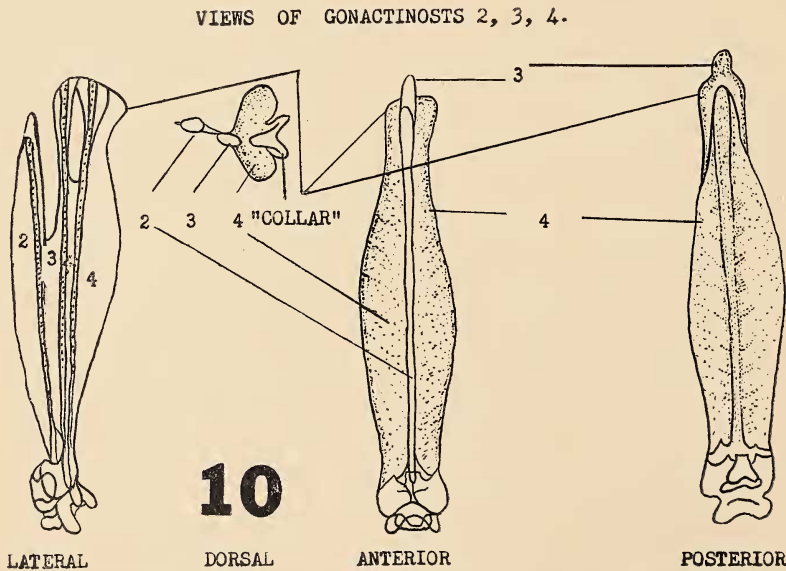
Sexual dimorphism expressed in hemal spines in fishes other than viviparous cyprinodonts has been reported by Ford (1937). He says that in *Labrus mixtus* there is a marked difference in the relative size of the circular hemal canal of the first caudal vertebra, this being larger in the male than in the female. He also illustrates the sexual difference in the condition of the hemal arch of the first caudal vertebra in *Labrus bergylta*, calling attention to the fact that in the male there are two canals but in the female one only. His figures also show another type of dimorphism which he does not mention; namely, the hemal spine is forked

ventrally in the male, but lanceolate in the female. The forked nature of the male's hemal spine has been seen in some cyprinodonts, too; in *Molliensia* for example, according to the figure in Hollister (1940); and Scott (1944) shows a somewhat similar structure in *Lebistes*. Undoubtedly there are many instances of sexual dimorphism expressed in hemal spines which have not yet been recorded, both in cyprinodonts and in other groups.

#### *Effects of Sex Hormones.*

Experiments designed to analyze the effects of sex hormones in gonopodium development were performed before studies were made of their effects upon suspensorial elements. For the work upon the gonopodium, Grobstein (1940, 1942) has a complete report on normal and treated *Platy-poecilus maculatus*, except for the brief statement of Grumbach (1935) which is based on his extensive but unpublished work on the regeneration of the anal fins without the use of hormones (1935b) and the unpublished thesis of Tasker (1934). Now, the work of Cummings (1943) on *Molliensia* should also be added.

Turner (1941, 1942) described the normal morphogenesis of the gonopodium and its suspensorium in *Gambusia* and was the first to report in detail the effects of androgens upon the development of the latter in females. This was followed closely by the studies of Cohen (1942) whose unpublished results were reported, in part, by Gordon, Cohen and Nigrelli (1943); these studies indicated that the gonopodium, its suspensor-



TEXT-FIG. 10. *Xiphophorus montezumae*. An example of the typical fusion of the gonactinosts 2, 3 and 4, developed in males only.



ial elements and modification of the caudal fin in *P. maculatus*, may be induced in females by the synthetic steroid pregnenolone. Scott (1944) reported hormonal effects on the *Lebistes* suspensorium.

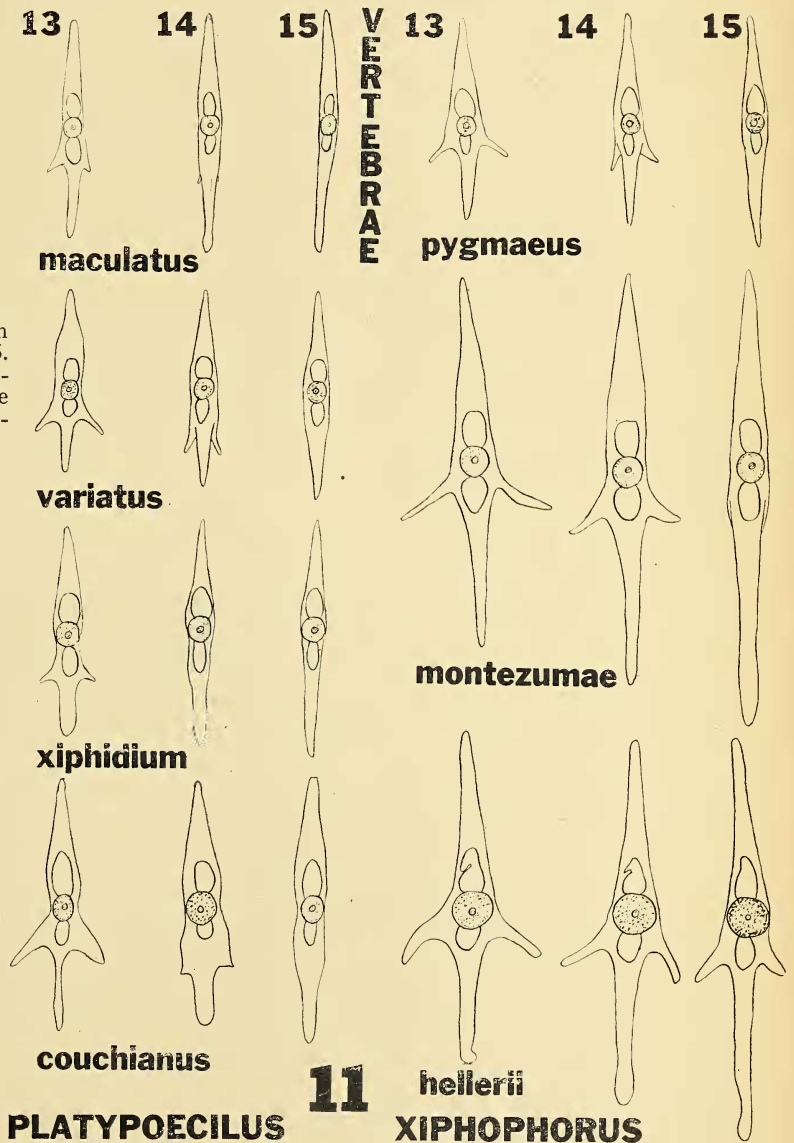
Thus it may be seen that the number of references to the effects of sex hormones upon skeletal elements recently reviewed by Gardner and Pfeiffer (1943) may be extended considerably, as far as fishes are concerned.

*The Bearing of Gonopodial and Suspensorial Characters upon Taxonomy.*

After the work of Garman, Phillipi and Langer up to 1914, interest in the elements of the gonopodial suspensorium for taxonomic purposes was revived by Howell

Rivero and Hubbs (1936) in their redescrptions of *Furcipennis huberi* (Fowler) and *Alfaro cultratus* (Regan). Hollister (1940) worked out a key to the cyprinodonts of Bermuda utilizing the characters of the gonopodial suspensorium. A somewhat similar study was made by Howell Rivero and Rivas (1944) for some of the cyprinodonts of Cuba. These workers reviewed the extensive use of gonopodial characters alone in taxonomy by Regan (1913) and Hubbs (1924) and earlier systematists.

In 1913 both Regan and Langer, working independently, pointed out that species of *Xiphophorus* and *Platypoecilus* were more closely related than had previously been suspected. Regan relied upon the characters of the gonopodia whereas Langer referred to



TEXT-FIG. 11. Xiphorhynchus Vertebrae: 13, 14, and 15. Anterior views of disarticulated vertebrae to show the first, second and third gonapophyses.

TABLE III. Regional Analysis of the Xiphophorin Vertebral Column in Males.

Species	No.	Pre-caudals	Caudals						Grand Total	
		Ribs only	Ribs only	Ribs and gonapoph.	Gonapoph. only	Hemal spine	Total	Average	Totals	Average
<i>P. maculatus</i>	8	11	1	1	2	11	15	14.9	26	25.9
	1	11	1	1	2	10	14		25	
<i>P. variatus</i>	10	11	1	1	2	12	16	16.3	27	27.3
	4	11	1	1	2	13	17		28	
	1	12	1	1	2	12	16		28	
<i>P. xiphidium</i>	13	11	1	1	2	12	16	15.7	27	26.6
	3	11	1	1	2	11	15		26	
	2	11	?	1	2	12	15		26	
	2	10	?	1"	2	12	15		25	
<i>P. couchianus</i>	9	11	1	1	2	12	16	16.2	27	27.2
	2	11	1	1	2	13	17		28	
<i>X. pygmaeus</i>	11	11	1	1	2	12	16	15.9	27	26.9
	1	11	1	1	2	11	15		26	
<i>X. montezumae</i>	10	11	1	2	1	13	17	17.0	28	28.0
<i>X. hellerii</i>	5	11	1	3	1	12	17	16.9	28	27.9
	5	11	1	3	0	13	17		28	
	1	11	1	3	1	11	16		27	
	(Cordova)	2	11	1	2	1	13	17		28

'=Gonapophysis detached, located below the 11th precaudal.

"=Gonapophysis detached, located below the 9th precaudal.

gonopodial and suspensorial features. Regan in associating *Xiphophorus* with *Platy-poecilus*, separated them off as a distinct group from other poeciliids. (This group later became the tribe *Xiphophorini*, Hubbs, 1924b). Langer's conclusion was more radical than Regan's. He suggested that members of the *Xiphophorus-Platy-poecilus* group be placed under a single genus.

Undoubtedly both Regan and Langer were influenced in making their decisions concerning the closeness of *Xiphophorus* to *Platy-poecilus* by the knowledge that *X. hellerii* (= *strigatus*) and *P. maculatus* were capable of hybridization and that many of their hybrids were fertile. Both men referred to the journals devoted to aquarium fish-culture: *Blätter für Aquarien und Terrarienkünde* and *Wochenschrift für Aquarien und Terrarienkünde*. These periodicals contained many stories concerning the rearing, breeding and hybridization of the platyfishes and swordtails during the years 1909 to 1913. A historical statement on this phase of the problem may be found in a paper by Gordon (1931).

#### The Major Vertebral Regions.

The vertebral column of fishes has been variously divided and subdivided by divers authors depending upon the complexity of the elements and the requirements of the analysis. The one major division all analysts use is the separation of the precaudal ver-

tebrae from the caudals. A generalized definition of a typical precaudal or caudal is unsatisfactory since vertebral details vary from one major group to another. A definition based upon the presence or absence of ribs is unsuitable. In some species like *Gadus*, according to Thompson (1917), and the anchovy, *Anchoa compressa*, according to Chapman (1944), the bearing of ribs stops at the last precaudal. Many species have this arrangement. Many do not: *Salmo*, according to Parker and Haswell (1897) has ribs on its first six caudal vertebrae and *Sardinops caerulea* has ribs on its first ten caudals, according to Phillips (1942). On the other hand, many of the posterior abdominals (precaudals) of *Xiphias*, for example, do not bear ribs, according to Gregory and Conrad (1937). Raven (1939) points out that the ribs in *Diodon* and *Masturus* are entirely lost and Dr. C. M. Breder, Jr., tells us that ribs are wanting in all species of the Molidae, Diodontidae and Tetradontidae.

Viviparous cyprinodonts have rib-bearing caudal vertebrae: *Flexipenis* has four and *Alfaro* has six such caudals according to Howell Rivero and Hubbs (1936). Thus rib-bearing vertebrae are not necessarily caudal or precaudal.

In view of these details the presence or absence of ribs in xiphophorin species cannot be used to determine the type of vertebra in question, for *X. hellerii* has a pair of

TABLE IV.

From Langer (1913)	Page 254	Page 263
Name	Zahl der regulären Hámápopophysen zu den Überganshamápopophysen, zu den Gonápopophysen ohne Rippe, zu denen mit Rippe, zu den Kumpfwirbeln nur mit Hámákanal, zu den typischen Rumpfwirbeln des ♂	(Erste Zahl=Wirbel ohne Rippen, zweite Zahl=Wirbel mit Rippen, D=Differenz) ♂
<i>Platypoecilus maculatus</i>	(2 mal) 10:0:3:1:0:12=26 (1 mal) 11:0:3:1:0:14=29	D.3 14:15=29 13:13=26 13:15=28
<i>Xiphophorus strigatus</i>	x <sup>1</sup> 13:0:0:3: 12=28 14:0:0:2:0:12=28 x (vor x <sup>1</sup> ) 14:0:0:3:?:11=28 x (vor x <sup>1</sup> ) 15:0:0:3:0:10=28 x (vor x <sup>1</sup> ) 13:0:1:2:?:12=28 x (vor x <sup>1</sup> ) 14:0:1:2:?:13=30 x (vor x <sup>1</sup> ) 15:0:1:2:?:12=30	D.2 13:15=28 14:14=28 15:13=28 15:15=30 18:11=29 16:13=29 16:14=30

x<sup>1</sup>=unerwachsenes Männchen (from another table on page 230-231).

ribs on each of its three gonapophysis-bearing vertebrae; *X. montezumae* has two pairs of ribs and the others have but one pair at comparable points. However, Langer (1913) has used this criterion in his analysis, Table IV.

Ford (1937), in illustrating a typical abdominal and caudal vertebra in *Anguilla* and *Conger*, shows that the precaudal, like that of *Gadus*, has widely open parapophyses, while the anterior caudal not only has a closed hemal arch, but that arch is extended into a produced hemal spine. Jordan (1905) says that a vertebra having hemal as well as neural spines is known as a caudal vertebra. Such a definition does not hold for some members of the Order Heterosomata. For those groups in which, like the Gadidae, the differences between the caudals and precaudals are sharp, there is a further complication of asymmetry. Ford points out that not infrequently it will be found that between the typical abdominal vertebrae and the typical anterior caudals there is a transitional form of vertebra which on the one side exhibits the characters of an abdominal vertebra and on the other side the characters of a caudal vertebra.

For our purposes the presence of a closed hemal arch plus its produced hemal spine will serve to determine the first caudal vertebra. On this basis, since the first hemal spine (the first gonapophysis in adult male Xiphophorini), develops from the ventral surface of the thirteenth vertebra, the thirteenth becomes the first caudal.

However, Turner's demonstration, through morphogenesis, that the ligastyle is in reality a modified and detached hemal spine, introduces an important factor in attempts to determine the point of separation of the

true caudal and precaudal vertebrae in viviparous cyprinodonts.

In *Gambusia affinis*, which has one more anterior vertebra than the xiphophorins, Turner has shown that the thirteenth vertebrae of juveniles and a few adult females bear closed hemal arches and spines while the same vertebrae of adult males and most adult females bear open hemal arches and no spines: in most adults, the fourteenth vertebrae bear closed hemal arches and spines. Obviously the conditions expressed earlier should determine the designation of the true caudal and precaudal for *Gambusia affinis*; the true point of division comes between the thirteenth and fourteenth. This illustrates another type of transitional vertebrae previously discussed.

In *P. maculatus* and *X. hellerii* Langer had previously shown that in young males, the "skeletstab" lies just in front of the presumptive first gonapophyses. These spinous bones do not appear, according to his figures, to be different in shape nor in size from the next hemal spines. In later stages, they become modified into typical ligastyles and are found more forward. Additional examples of transitional vertebrae may be seen in the anomalous specimens of *P. xiphidium*, previously described in detail, in which the ligastyles were either missing or atrophied and their positions were taken by detached hemal spines of the caudal vertebrae next in series. It seems, therefore, that the ligastyles in *Platypoecilus* and *Xiphophorus* have the *Gambusia affinis* type of morphogenesis, except for this detail: the xiphophorin ligastyles develop from the twelfth vertebra.

Thus on the basis of the above discussion, we have decided, perhaps arbitrarily, to call

the twelfth vertebra of xiphophorins the first true caudal, and every one anterior to it, precaudal. The first gonapophysis-bearing vertebra, the thirteenth, is the second caudal vertebra.

#### *Vertebral Counts and Source of Specimens.*

Langer listed the total number of vertebrae in detail of *P. maculatus* and *X. hellerii*. Since Langer's data do not agree with ours, Table III, it is desirable to reprint his as he presented them for purposes of discussion, Table IV.

He reports four gonapophyses in *P. maculatus* and two or three in *X. hellerii*. We find three gonapophyses constantly in the former and three or four in the latter. Garman (1895) reported that *X. hellerii* had four or five "stays," one of which may have been an incompletely developed ligastyle.

We agree that, in *Platypoecius maculatus*, the first gonapophysis is the only one that bears a pair of ribs. We disagree on the number of rib-bearing gonapophyses in *Xiphophorus*: Langer records that four specimens out of seven have only two rib-bearing gonapophyses; we find that all the specimens from the Rio Papaloapan have three gonapophyses-bearing ribs. However, we indicate that two of our *X. hellerii* from Cordova (Rio Blanco) have the arrangement reported by Langer.

We believe that one of the reasons, probably the most important, for our disagreement lies in the dissimilar sources of the materials. We are aware that small but consistent differences may be found in geographically isolated populations of the same species or subspecies. We were careful to present the natural source of our specimens. Langer states in his introduction that his specimens came, for the most part, from aquarium-fish dealers, mentioning among others, probably the largest and most famous one in his day and place, Frau Bertha Kuhnt, Conradshöhe bei Tegel-Berlin.

In his history of the platyfish and swordtails under domestication, Gordon (1931, 1937) pointed out that the platyfish were first imported into Germany in 1907, to be followed by the swordtails in 1909. During 1910 and thereafter up to the first World War, many reports of hybridization of these species appeared yearly in the aquarium journals. One of the hybrids between *P. maculatus* and *X. hellerii* had been backcrossed so often to the swordtail that Regan (1911) took it to be a new species, describing it as *Xiphophorus rachovii* Regan, only to recall the name after realizing its hybrid origin in the aquarium. Thus it is definitely possible that Langer worked with *P. maculatus* containing some *X. hellerii* genes and *X. hellerii* containing some *P.*

*maculatus* genes. Preliminary study of our own genetically known hybrid material indicates a breakdown in the usually consistent patterns of the vertebral columns in pure species.

Another possibility to account for our lack of agreement in total vertebral counts and other details may be that Langer's specimens came from localities in Mexico other than those recorded by us. We indicated that the *X. hellerii* from the Rio Blanco (to be sure only two specimens were available) differed from those of the Rio Papaloapan. Many isolated geographical populations differ in their genetic constitution, sufficiently so that they may be recognized according to the preliminary report of Gordon (1943) on the xiphophorins.

Finally, six of the seven specimens of the swordtail studied by Langer were immature. The one adult he analyzed agrees with our material.

We fail to understand the lack of correlation between the total vertebral counts in Langer's two tables, in view of the circumstances that the number of specimens listed in each table is the same, Table IV.

#### *Analysis of Vertebral Column.*

An analysis of the regional differentiation of the vertebral column in the seven xiphophorin fishes reveals that the precaudal section is essentially uniform in all. With the exception of one *P. variatus* and two anomalous specimens of *P. xiphidium*, all the rest of the 82 Xiphophorini studied have eleven precaudal vertebrae and the ligastyles are located beneath the tenth ones.

Differentiation of the xiphophorin vertebral column takes place in the caudal region. Here differences involve (1) the number of caudal vertebrae, (2) the number of anterior caudal vertebrae with ribs and gonapophyses, (3) the number of anterior caudal vertebrae with gonapophyses alone, and (4) the presence and nature of the apophyseal projections from the vertebrae or gonapophyses. It is significant that all types of variations appear in the caudal vertebrae. It is just these vertebrae which are particularly susceptible to variation in numbers in response to changes in temperatures and possibly other environmental agents during the developmental stages of fishes. Hubbs (1922, 1942a) pointed out that in *Notropis atherenoides*, *N. hudsonius* and *N. blennioides*, the number of caudal, not the precaudal, vertebrae are affected by change in temperature during their development stages; the higher the temperatures during that critical period, the fewer caudal vertebrae developed. The same effect has been found in the herring by Ford (1933). Gabriel (1944), too, has demonstrated that the total verte-

bral counts in *Fundulus* reflect a similar response to temperature levels during the embryonic stages. His more important demonstration was showing proof that there are genetic factors present which play a dominant part in controlling the number of vertebrae. Some sib-ships, he reported, are temperature-labile and some are not. In other words there are some groups possessing hereditary factors which find expression regardless of, or in response to, high or low temperatures.

We know that *P. maculatus* and *X. hellerii* live together in portions of the Rio Papaloapan and in our laboratory under similar temperature conditions; yet platyfish have 15 caudal vertebrae while the swordtails have 17. This reflects part of the sum total of genetic differences between these species. These details also suggest that the platyfish has a more rapid rate of development. This seems to be borne out by data published by Bellamy (1924) who stated that the average interval between broods for *P. maculatus* is 31 days; for *X. hellerii*, 39 days. The meaning of "interval between broods" probably needs some explanation. For some time many of us thought that the interval between broods represented the full time of gestation. However, Hopper (1943) has found that in *P. maculatus* fertilization of the eggs takes place not immediately after the birth of the previous brood, but about seven days after. Thus the gestation period in platyfish is about 24 instead of 31 days. Unfortunately similar kinds of data are not available for the swordtail, but it is likely, in view of its longer "interval between broods," that its gestation period is longer than that of platyfish.

To allow for any possible future need for correction, the following is put on the record: Bellamy's data were obtained from cultivated fishes. The wild stocks used in our laboratory originated, as indicated under "Material and Methods," in Plaza de Agua, Rio Jamapa, Veracruz, for the platyfish; and headwaters of the Arroyo Zacatispan (tributary of the Rio Papaloapan), Oaxaca, for the swordtails. There is no appreciable difference in the dorsal fin-ray count for platyfish populations of the Rio Jamapa and the Rio Papaloapan systems, although the two populations may be told apart on the basis of the distributions of their gene frequencies, genes that control their color patterns, Gordon (1943).

The habitat of *P. variatus*, *X. pygmaeus* and *X. montezumae* is the Rio Panuco system. In one of its tributaries, the Rio Axtla, just at the village of Axtla, San Luis Potosi, the three species may be found in the same cross-section of the stream. Other conditions of their special ecology are different:

*X. pygmaeus* are found in pure colonies, numbering in hundreds, only along the cut-in slope where the water is deep and runs in a strong current; *P. variatus* and *X. montezumae* are found in the slip-off section of the stream, in shallow, slow waters, often in pools alongside the banks. If the field notes of the collections are studied closely, a further breakdown of the ecological condition of *P. variatus* and *X. montezumae* becomes evident, for the greater numbers of *P. variatus* are to be found downstream, while *X. montezumae* outnumber the platyfish upstream. This distinction in population composition of the two species may be seen in localities of the same stream only two or three miles apart. At the time the collections were made there was no appreciable difference in the temperatures at these various localities. The vertebral number in the caudal region is genetically set: 17 for *X. montezumae*, about 16.3 for *P. variatus* and about 15.9 for *X. pygmaeus*. The specific localities of the stocks used is given elsewhere, while they are all found in waters of about the same temperature. It is likely that on a basis of yearly average temperatures, *X. pygmaeus* is subject to the lowest temperatures, while *P. variatus* is subject to the highest.

Going back for a moment to the general problem of variation in vertebral counts in response to changes in temperatures and other agents during the developmental stages of fish, we find that this reaction has, as yet, not been correlated with the finding of Hyman (1921) that during the development process in the teleost *Fundulus*, a secondary region of high physiological activity (metabolic gradient) arises at the posterior end and persists for some time.

An interesting problem suggest itself—of studying at just what developmental period the number of vertebrae may be affected by temperature changes. From the available information, it would seem that the developmental stages during somite formation might be the critical ones.

#### *The Degrees of Specialization.*

Howell Rivero and Hubbs (1936) have made a preliminary evaluation of the degrees of specialization in three tribes of cyprinodont fishes: Alfarini (*Furciferis* and *Alfaro*), Poeciliini (perhaps referring to *Lebistes* and *Mollienisia*) and Xiphophorini (*Xiphophorus*). They state that the gonopodial suspensoria of the Alfarini are strikingly unlike those of the Poeciliini, being much less specialized; they are, however, very similar to that of the *Xiphophorus*. This resemblance they believe indicates a primitive origin for the Alfarini and *Xiphophorus* but does not definitely indicate any very

close relationship between the Alfarini and the Xiphophorini.

In estimating the degrees of specialization in the gonopodial suspensorium, Table II and the following criteria may be used:

1. The degree of masculinization of each of the three hemal spines of the first three anterior caudal vertebrae.

2. The degree of masculinization of the interhemals, 1, 2, 3, 4 and 5.

3. The presence of ribs on the first three anterior caudal vertebrae.

If minimal changes seen in male's hemal spines over the homologous structures in juveniles or in unmodified females indicate primitiveness, then *X. hellerii*, *X. montezumae* and *P. maculatus* are the most primitive.

Concerning the interhemals, if much fusion of 2, 3 and 4 is a measure of specialization, then all the *Xiphophorus* are more highly developed; if the dorsal tip of the fourth gonactinost when modified into a "collar" indicates complexity of structures, then *P. maculatus* and *P. variatus* are the more primitive forms.

If the presence of a pair of ribs on each of the first three anterior caudal vertebrae is an indication of primitiveness, then *X. hellerii* is most primitive, with three pairs, *X. montezumae* second with two, and the rest the most specialized with but one rib.

It would be shortsighted to base any new revision upon characters of any one limited group of morphological units, and no attempt is made in this paper to change the present arrangement of species which might be based upon the many details described. One could easily make out a case in support of Regan's conclusions or those of Langer. We prefer to postpone our final decision until all the many known facts concerning the group are evaluated. In the final analysis the important matter is not to decide whether these fishes represent one or two genera but rather to gain detailed information concerning the constitution of each member of the group.

#### SUMMARY.

(See also Table II).

The sex-modified hemal and interhemal spines that make up the gonopodial suspensorium are analyzed for the seven species of xiphophorin fishes. The hemal spines of the first three, anterior, caudal vertebrae are masculinized into gonapophyses and directed forward rather than backward. They are of various shapes and in most instances more massive than ordinary hemal spines. The second gonapophyses are the most specialized.

In relation to the serial number of the vertebrae, the first caudal is usually the twelfth. In all but *Xiphophorus hellerii* which has a pair of ribs on its 13th, 14th and 15th vertebrae and *Xiphophorus montezumae* which has a pair of ribs on its 13th and 14th vertebrae, all the rest have one pair of ribs on their 13th vertebrae only. *Xiphophorus pygmaeus* is the only sword-tail that has greatly extended parapophyses on its first gonapophysis and greatly extended uncinatoid processes on its second.

The masculinized actinosts or pterygiophores, 1, 2, 3, 4 and 5 (out of the nine), are called gonactinosts. Gonactinosts 2, 3 and 4 are variously fused. Gonactinosts 3 and 4 are rarely fused at their tips in the species of *Platypoecilus*; they are rarely separate in *Xiphophorus*.

On the basis of measurements of the gonapophyses in the four species of *Platypoecilus* with respect to length of spine, width of spine, length of uncinatoid processes and the degree of spread of the uncini, it is possible to identify the characteristic features in *P. maculatus*, *P. variatus*, *P. xiphidium* and *couchianus*.

The origin of a spinous bone within a ligament connecting the ventral surface of vertebra 10 and the compound gonactinosts is discussed and the structure named, *ligastyle*.

Discussions cover the degrees of specialization within the group in relation to other cyprinodont fishes, the bearing of gonopodial and suspensorial characters upon taxonomy.

The paper contains an analysis of the regional differentiation of the vertebral column in xiphophorin fishes and this is related to the genetic constitution of the species and to the special ecology of the fishes in their natural waters.

Descriptions of anomalous specimens are presented together with descriptions of sexual dimorphism in hemal spines in fishes other than cyprinodonts.

Figures illustrate the gonopodial suspensoria of each of the seven xiphophorins, showing the relationship of the gonapophyses to the gonactinosts and to the gonopodia. The gonapophyses are presented in lateral and anterior views.

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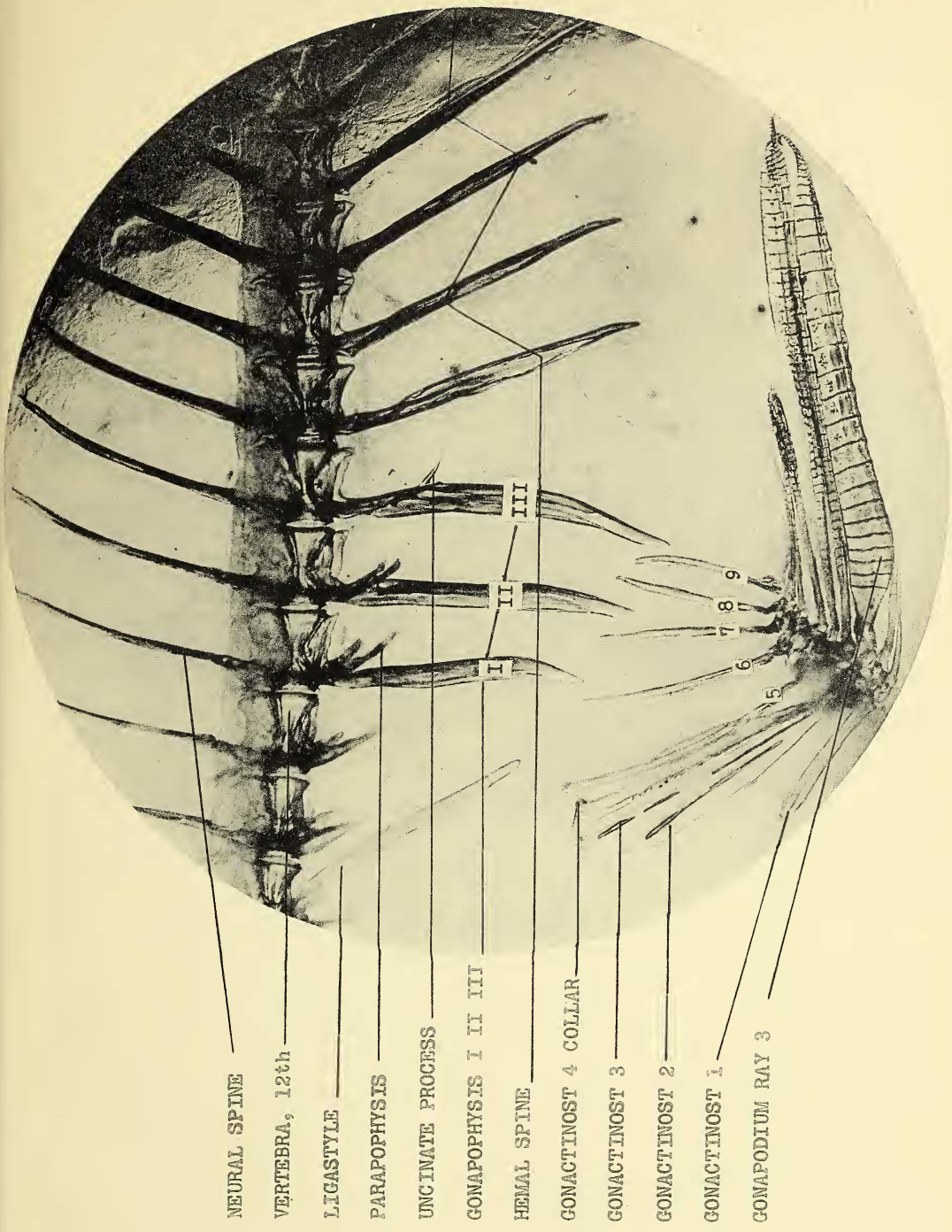
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## EXPLANATION OF THE PLATE.

### Plate I.

The Gonopodium and Its Suspensorium of *Xiphophorus montezumae*.





SEXUAL DIMORPHISM IN THE SKELETAL ELEMENTS OF THE GONOPODIAL SUSPENSORIA IN XIPHOPHORIN FISHES